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INHERITANCE OF OLEIC, LINOLEIC AND LINOLENIC ACIDS IN SEED OIL OF RAPESEED (*BRASSICA NAPUS* L.)

by

© PHILLIP MAURICE THOMAS

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

IN

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EDMONTON, ALBERTA

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Inheritance of Oleic, Linoleic and Linolenic Acids in Seed Oil of Rapeseed (Brassica napus L.)" submitted by Phillip Maurice Thomas in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

The oleic, linoleic and linolenic acid content of rapeseed (Brassica napus L.) oil was investigated in self- and cross-pollinated seed on parental lines and reciprocal F_1 and F_2 populations. The seed was derived from three crosses from three strains of rapeseed that produce seed oil practically free of eicosenoic and erucic acids and differing in oleic, linoleic and linolenic acid content. A definite maternal genotype effect on the oleic and linoleic acid content of the cross-pollinated seed was evident in two of three crosses. Embryo control for the quantities of these two fatty acids was indicated for the third cross. Both embryo and maternal genotype control of linolenic acid content was indicated. There were no cytoplasmic effects evident in the reciprocal F_1 and F_2 populations for any fatty acid in all three combinations.

The F_1 population values indicated that the oleic and linoleic acid contents were controlled by a simple additive gene system in one cross. In the other two crosses, partial dominance for high oleic and low linoleic content was observed. Dominance of low linolenic acid values was observed. The heritability estimates for oleic and linoleic acid were similar within each cross. The heritability estimates ranged from 53% to 78% for oleic, 40% to 84% for linoleic and 26% to 59% for linolenic. The estimates of minimum number of effective factors controlling oleic, and linoleic were similar within each cross. The number of effective factors ranged

from 2 to 6 for oleic, 3 to 5 for linoleic, and 0 to 4 for linolenic. The similarity of genetic behavior of oleic and linoleic acid content within each cross and the very high negative correlation between these components indicates that the relative ratios of oleic and linoleic acid content may be under the control of one genetic system.

The variable effect of maternal and embryo genotype on the fatty acid composition complicates the effectiveness of the "half-seed" breeding technique.

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INTRODUCTION

Rapeseed has become Canada's most important edible oilseed crop. Rapeseed, as an oilseed crop, was first grown commercially in Canada in 1942. Black Argentine rape (Brassica napus L.) was imported from Argentina for production in western Canada (Downey and Bolton 1961).

Production of rapeseed is centered in the prairie provinces where acreage has grown from 3,200 acres in 1943 to a maximum of 5,306,000 acres in 1971. Two species of rapeseed are grown in western Canada; Brassica napus, commonly referred to as the Argentine type and (Brassica campestris L.), commonly referred to as the Polish type or turnip rape. Only the summer forms of both species are grown in western Canada. The winter forms are not sufficiently winter hardy for western Canadian conditions. Brassica napus is largely self-pollinated while Brassica campestris is self-incompatible and therefore cross-pollinated. Brassica campestris production accounts for approximately 75 percent of the rapeseed acreage of western Canada.

Canada is a major producer of rapeseed. Rapeseed is fourth in importance in world production of edible oils after soybean, sunflower and groundnut. Rapeseed accounts for approximately 8 percent of the total exports of edible vegetable oils and Canada's share of world exports of rapeseed is about 33 percent (Porteous and Johnson 1970).

The world edible oilseed market is very competitive due to the interchangeability of different oils. Among these are soybean, sunflower, groundnut, corn, cottonseed and safflower oils. Improvement in Canada's competitive position can best be achieved by improving the

quality of rapeseed oil and meal, and efficiency of production. The quality of edible rapeseed oil is largely determined by its fatty acid composition. The major fatty acids in most edible oils are oleic and linoleic. Traditional rapeseed oils differ from other edible oils in that they contain a high percentage of eicosenoic (9 - 15%) and erucic (20 - 45%) acids. The Canadian federal government in 1970 deemed it desirable to eliminate eicosenoic and erucic acid from rapeseed oil to improve its nutritional value. Through advances in plant breeding, Canadian cultivars in both species have been developed that produce oils practically free of eicosenoic and erucic acid.

Two of the present rapeseed breeding objectives are the reduction or elimination of linolenic and the increase of linoleic acid content. It was suggested by Downey (1966), that removal or reduction in the level of linolenic acid would reduce processing costs, increase the shelf life of the oil and place it in a premium quality class. An increase in linoleic acid content should provide a better balanced composition for human nutrition.

Few studies have been reported on the inheritance of the fatty acids oleic, linoleic and linolenic in rapeseed oil. Knowledge of the inheritance of these components and their interrelationships is necessary for a plant breeder to efficiently plan his breeding program.

This study was undertaken to gain a better understanding of the nature of the inheritance of the major C-18 fatty acids in low erucic acid rapeseed (B. napus) oil.

LITERATURE REVIEW

The application of gas-liquid-phase chromatography to the analysis of mixtures of saturated and unsaturated fatty acids was reported by Craig and Murty (1958). This analytical procedure was found to be useful as a rapid and reliable means of selecting for fatty acid composition in rapeseed (Craig 1961).

Study of western Canadian grown rapeseed varieties showed that fatty acid variation in Argentine-type (Brassica napus L.) varieties occurred in oleic (10.2 - 23.1%), erucic (40.0 - 49.2%), linoleic (10.4 - 17.2%), linolenic (5.4 - 9.4%) and eicosenoic acids (12.1 - 15.1%) (Craig and Wetter 1959). Variation in Polish-type (Brassica campestris L.) varieties occurred in oleic (21.3 - 35.9%), erucic (22.4 - 37.2%), linoleic (15.0 - 19.8%), linolenic (6.0 - 9.1%) and eicosenoic acids (11.8 - 15.8%) (Craig and Wetter 1959). A similar study confirmed that major variation occurred in oleic, linoleic and erucic acid content. Significant variation among locations for all fatty acids and among varieties for each fatty acid except linolenic were observed (Craig 1961). The significant differences among locations for all fatty acids indicated a marked environmental effect.

Erucic acid was the first fatty acid to be investigated for genetic variability. Inbreeding and selection for low erucic acid values resulted in the isolation of strains of B. napus (Stefansson et al. 1961) and B. campestris (Downey 1964) with seed oil containing less than 1% erucic acid. The decrease in erucic acid produced a simultaneous decrease in eicosenoic acid. The decrease in the level of eicosenoic and erucic acids resulted in an increase in oleic and linoleic acids (Downey and Craig 1964).

Reciprocal crosses between rapeseed plants (B. napus) containing low erucic and high erucic acid demonstrated that erucic acid content was controlled by the genotype of the embryo rather than that of the maternal parent (Downey and Harvey 1963). Because of the high negative correlation between oleic and erucic acid percent (Downey and Craig 1964), the oleic acid percent is also controlled by the genotype of the embryo if varying amounts of erucic acid are present. The erucic acid content of B. napus (summer type) seed oil is controlled by a two gene system acting in an additive manner (Harvey and Downey 1964). Each allele for high erucic acid contributes 9 to 10% erucic acid. These results were confirmed in a similar study which also found that eicosenoic acid content is controlled by the same two gene system with the alleles for high eicosenoic acid acting in a dominant manner (Kondra and Stefansson 1965). The level of eicosenoic acid in seed oil of B. napus was maintained at 12 to 14% in all but the low erucic acid genotype where levels of 1 to 3% were reported.

The erucic acid content of seed oil in B. campestris is conditioned by a single gene system acting in an additive manner. The fatty acid composition of the seed is controlled by the genotype of the embryo (Dorrell and Downey 1964).

The embryo constitutes approximately 85% of the mature seed weight with only a single cell layer of endosperm and a thin seed coat of maternal tissue. Since the oil is stored within the embryo, one would anticipate embryo genotype control of fatty acid composition. However, maternal effect has been reported in rapeseed (B. napus) oil (Kondra and Stefansson 1970). The unsaturated C-18 fatty acids are influenced by both maternal and embryo genotype in low erucic acid lines.

Eicosenoic and erucic acids are formed by a genetically controlled carbon chain elongation pathway operating by the addition of acetate molecules to the carboxyl end of oleic acid (Downey and Craig 1964). The linoleic and linolenic acids are formed by a separate desaturation pathway with oleic acid as a precursor (Downey 1966). The selection of strains of rapeseed with seed oil practically free from erucic and eicosenoic acids was through the detection of a genetic block between the oleic and eicosenoic acids in the elongation pathway. No genetic blocks have as yet been reported in rapeseed in the desaturation pathway.

Maternal effects on fatty acid composition of seed oil have been observed in other oil seed crops which store their oil in the embryo. The main constituents of the oils from these crops are the 18-carbon, unsaturated fatty acids; oleic, linoleic and linolenic. The maternal effects have generally been studied at two levels. The first is the study of the fatty acid composition of self- and cross-pollinated seed on parental lines. The second is the analysis of the fatty acid composition of seed from reciprocally different F_1 and F_2 populations. Analysis of self- and cross-pollinated seed on parental corn lines indicated that the maternal parent significantly influences the fatty acid composition in some crosses but not in others (Jellum 1966). The study of reciprocal F_1 and F_2 populations of corn indicated that some cytoplasmic effect was evident for linoleic and oleic acid content (Poneleit and Bauman 1970; de la Roche et al. 1971). The oleic, linoleic and linolenic content of flaxseed oil is determined largely by the genotype of the embryo but is affected by the genotype of the maternal parent to a limited extent (Yermanos and Knowles 1962). A

similar study in safflower indicated complete embryo control of oleic and linoleic acid content (Knowles and Hill 1964). However, oleic, linoleic and linolenic acid content in soybean is largely controlled by the maternal parent (Brim et al. 1968).

A study of linoleic acid in soybean seed oil indicated that inheritance was quantitative with a continuous range of variation in F_2 populations (White et al. 1961). In safflower seed oil, however, a single locus controls relative oleic and linoleic acid content with the allele for high linoleic acid partially dominant (Yermanos et al. 1967). Stearic acid content of safflower seed oil is largely under the control of two alleles at a single locus with the allele for low stearic acid values partially dominant (Ladd and Knowles 1970).

Genetic control of fatty acid composition in corn oil appears to be quite variable. A single dominant gene conditioning low linoleic and high oleic acid was reported for corn (Poneleit and Alexander 1965). A second locus and possible modifier genes with small effects were later proposed after study of similar genetic materials (de la Roche et al. 1971). Dominant, additive and heterotic effects for various fatty acids in corn oil were reported from a study of inbreds and reciprocal crosses (Jellum 1966). Another study indicated that genetic variation of fatty acid composition was found to be due primarily to additive gene effects (Poneleit and Bauman 1970). A single partially dominant gene was reported to control low linoleic acid (Poneleit 1972).

In flax seed oil, partial dominance was indicated for low linolenic acid content and high oleic acid content (Comstock et al. 1960). Analysis of non-segregating and segregating populations in flax indicated that percentages of oleic and linolenic acids were highly

heritable when field grown populations were analyzed. However, heritability was greatly decreased when the same populations were studied in growth chambers (Comstock et al. 1960).

Several authors have presented correlation coefficients for pairs of fatty acids in rapeseed oil containing erucic acid. Correlation coefficients for the fatty acid pair oleic and erucic indicated a strong negative association in B. napus -.39 and -.78 (Gross and Stefansson 1966), -.98 (Craig 1961), -.99 (Downey and Craig 1964) and in B. campestris -.57 and -.66 (Gross and Stefansson 1966). Correlation coefficients for the fatty acid pair oleic and linoleic, indicated a close negative association in B. napus -.29 and -.86 (Gross and Stefansson 1966), -.85 to -.98 (Stefansson and Storgaard 1969) and in B. campestris -.15 and -.62 (Gross and Stefansson 1966). Correlation coefficients for the fatty acid pair oleic and linolenic indicated a negative correlation in B. napus -.30 and -.97 (Gross and Stefansson 1966), -.58 to -.70 (Stefansson and Storgaard 1969) and in B. campestris -.29 and -.79 (Gross and Stefansson 1966). Correlation coefficients for the fatty acid pair linoleic and linolenic indicated a positive correlation in B. napus .84 and .88 (Gross and Stefansson 1966), .31 to .55 (Stefansson and Storgaard 1969) and in B. campestris .71 and .96 (Gross and Stefansson 1966). These reported correlation coefficients indicated that oleic generally tends to be negatively correlated with other fatty acids, while linoleic and linolenic tend to be positively correlated when expressed as percent of total fatty acids.

Correlation coefficients for fatty acids expressed as percentage of seed weight were reported for the fatty acid pairs oleic and

linoleic -.10 to -.89, oleic and linolenic -.21 to .06, linoleic and linolenic .04 to .43 (Stefansson and Storgaard 1969). With fatty acids expressed as percent of seed weight there were no consistently significant correlations for any pair of fatty acids and negative correlations between oleic and other fatty acids were greatly decreased. Measuring fatty acids as percent of total fatty acids restricts the freedom for variation among fatty acids by making the sums of all of them equal to a constant 100%. When fatty acids are expressed as percent of seed weight a change in a major constituent of the oil can be accompanied by changes in the other major components such as protein and carbohydrate fractions of the seed. Therefore the tendency for negative correlation between fatty acids is greatly decreased.

Correlation coefficients for pairs of fatty acids in other oilseed crops showed that oleic and linoleic acid were closely negatively associated in safflower -.99 (Yermanos et al. 1967) and in corn -.97 (Poneleit and Bauman 1970). The fatty acid pair oleic and linolenic was highly negatively correlated in flax -.77 to -.97 (Comstock et al. 1960). The fatty acid pair linoleic and linolenic was highly positively correlated in one study of soybean .74 and .76 (Howell and Collins 1957), and had correlation coefficients ranging from .13 to .96 in another study (White et al. 1961).

MATERIALS AND METHODS

Plant Materials

Three strains of rapeseed (Brassica napus L.) which produce seed oil practically free of eicosenoic and erucic acid and differing in oleic, linoleic and linolenic acid content were used as parental lines. The fatty acid composition of the oil from self-pollinated seed from the parental lines is presented in Table 1.

Table 1. Fatty acid composition of oil from self-pollinated seed of three strains of rapeseed

Parent designation	Fatty acids as percent of total fatty acid					
	Palmitic	Oleic	Linoleic	Linolenic	Eicosenoic	Erucic
1	4.7	69.7	12.8	12.2	0.7	t*
2	4.9	54.2	27.4	12.0	1.7	t
3	6.0	42.6	35.6	15.2	0.5	t

* t = trace

Plants of the three strains were self-pollinated and cross-pollinated in all possible combinations to produce a diallel cross. Such an arrangement for n parental lines yields n(n - 1) crosses, reciprocals included. Parental and F_1 plants were bagged to produce self-pollinated parental seed and F_2 seed in the greenhouse. During the summer of 1971, the parental, F_1 and F_2 populations were grown in the field in 1.5 m rows, 0.3 m apart. The seeding rate was 50 seeds

per 1.5 m. The crosses between parental strains were repeated to produce cross-pollinated seed. Self-pollinated seed was produced on parental, F_1 and F_2 plants.

Fatty Acid Analysis

The fatty acid composition of the seed oil was determined by gas-liquid-phase chromatography. Samples consisted of 8 seeds for chemical analysis of self- and cross-pollinated seeds of parental plants. A bulk sample of 25 seeds was used for the analysis of self-pollinated seeds of F_1 and F_2 plants. Also, 50 single seeds were analyzed from F_1 plants from each cross. The methyl esters for gas chromatography were prepared by the method of Downey and Craig (1964).

A Hewlett Packard 5750 Research Chromatograph equipped with a hydrogen flame ionization detector was used for gas chromatographic analysis. Areas of the peaks were determined by the use of a Hewlett Packard 3370B Integrator. The areas of the gas chromatography peaks were used to calculate fatty acids as percent of total fatty acids. Column Specification:

Tube — stainless steel 1/8" x 8'

Solid Phase — Chromosorb G

Liquid Phase — butanediolsuccinate 4% by weight.

Only the following fatty acids were calculated: palmitic (16 carbon chain, saturated), oleic (C-18, monene), linoleic (C-18, diene), linolenic (C-18, triene), eicosenoic (C-20, monene) and erucic (C-22, monene). Minor constituents, such as the fatty acids stearic,

palmitoleic, arachidic, behenic, eicosodienoic and docosadienoic were not calculated in order to permit rapid analysis. Craig and Wetter (1959) reported that those minor constituents were present in amounts less than one percent each.

Statistical Procedures

Theoretical arithmetic means were calculated according to the methods suggested by Powers and Lyon (1941) (Table 2).

Table 2. Formulas for calculating theoretical arithmetic means

Population	Actual mean	Theoretical arithmetic mean
P_1	$\overline{P}_1$	$\overline{P}_1$*
P_2	$\overline{P}_2$	$\overline{P}_2$
F_1	$\overline{F}_1$	$(\overline{P}_1 + \overline{P}_2)/2$
F_2	$\overline{F}_2$	$(\overline{P}_1 + 2\overline{F}_1 + \overline{P}_2)/4$

* $\overline{P}_1$, $\overline{P}_2$, etc. represent the actual means of the P_1, P_2, etc. populations

Methods to determine dominance were suggested by Klambanonda (1950). If no dominance exists on an arithmetic scale then the actual

F_1 value would be equal to the mid-parent value, $(\bar{P}_1 + \bar{P}_2)/2$.

A scaling test was employed to test for genetic interaction between loci (epistasis). The scaling test was a joint scaling test developed by Cavalli (1952). Three parameters, m, d and h were estimated from the means of the two homogeneous strains and the F_1 and F_2 populations followed by a comparison of the observed generation means with expected values derived from the estimates of the three parameters. The three parameters were estimated by weighted least squares, taking as weights the reciprocals of the squared standard errors of each mean. The comparison between observed and expected means were then effected by assuming the sum of squares minimized in the fitting process to be distributed as a chi-square with degrees of freedom three less than the number of family means available (three less because three parameters have been fitted). If the actual means were found inadequate (non-additive) according to the scaling test, then transformation of the data may eliminate the non-additivity (Horner, Comstock and Robinson 1955; Falconer 1967).

Several methods were used to calculate estimates of "broad sense" heritability and the minimum number of effective factors controlling each fatty acid (Tables 3 and 4). The formulas of Table 4 furnishes an unbiased estimate of the minimum gene number when the following assumptions apply: (1) no linkage exists between pertinent genes, (2) one parent supplies only plus factors and the other only minus factors among those in which they differ, (3) all genes have equal effect, (4) the degree of dominance of plus and minus factors is the same for all, and (5) no interaction exists between pertinent non-allelic genes (Burton 1952).

Table 3. Formulas for estimating heritability (h^2)

Formula	Reference
$h^2 = \frac{VF_2 - VF_1}{VF_2}$ *	Burton (1951)
$h^2 = \frac{VF_2 - (VP_1 \times VP_2)^{1/2}}{VF_2}$	Mahmud and Kramer (1951)
$h^2 = \frac{VF_2 - 1/3(VP_1 + VF_1 + VP_2)}{VF_2}$	Weber and Moorthy (1951)

* VF_1, VP_1, etc. are variances of the respective populations F_1, P_1, etc.

Table 4. Formulas for estimating minimum numbers of effective factors (k)

Formula	Reference
$k = \frac{(\bar{P}_1 - \bar{P}_2)^2}{8(VF_2 - VF_1)}$ *	Castle and Wright (1921)
$k = \frac{(\bar{P}_1 - \bar{P}_2)^2}{8(VF_2 - 1/3(VP_1 + VF_1 + VP_2))}$	Weber (1950)
$k = \frac{.25(.75 - h + h^2)(\bar{P}_1 - \bar{P}_2)^2}{VF_2 - VF_1}$	Burton (1952)

* $\bar{P}_1$, $\bar{F}_1$, and $\bar{P}_2$ are actual means of the P_1, F_1 and P_2 populations respectively and VP_1, VF_1, and VP_2 are variances of the P_1, F_1 and P_2 populations respectively. $h = \bar{F}_1 - \bar{P}_1/\bar{P}_2 - \bar{P}_1$

RESULTS

Scaling Test

The Cavalli joint scaling test was applied to the original data for oleic, linoleic and linolenic acid content. The resulting chi-square values were highly significant for oleic, linoleic and linolenic acid values in all three crosses (Table 5). The significant

Table 5. Chi-square values for Cavalli joint scaling test for oleic, linoleic and linolenic acid content on original data

	Cross		
	1 x 2	1 x 3	2 x 3
Oleic	11.37**	22.88**	79.02**
Linoleic	6.64**	16.63**	32.46**
Linolenic	24.36**	9.47**	55.55**

** significant at 1% level

chi-square values indicate that the original scale was inadequate (non-additive) for all three fatty acids in all three crosses. Therefore, the original data was transformed to a log 10 scale. The joint scaling test was applied to the log 10 values. Significant chi-square values for oleic and linolenic acid content in all three crosses and for linoleic acid content in cross 2 x 3 were observed (Table 6).

Table 6. Chi-square values for Cavalli joint scaling test for oleic, linoleic and linolenic acid content on log 10 transformed data

	Cross		
	1 x 2	1 x 3	2 x 3
Oleic	13.16**	33.70**	77.63**
Linoleic	2.53	2.40	25.63**
Linolenic	32.53**	7.50**	43.30**

** significant at 1% level

The transformation of original data to a log 10 scale eliminated the non-additivity for only linoleic acid content in two of three crosses. Therefore, the original data was next transformed to angles, using the formula, angle = arc sine $\sqrt{\text{percentage}}$. The joint scaling test was applied to the angle values. Significant chi-square values for oleic and linoleic acid content in all three crosses and for linolenic acid content in crosses 1 x 2 and 2 x 3 were observed (Table 7).

Table 7. Chi-square values for Cavalli joint scaling test for oleic, linoleic and linolenic acid content on angle transformed data

	Cross		
	1 x 2	1 x 3	2 x 3
Oleic	10.59**	17.91**	71.34**
Linoleic	5.14*	9.04**	30.23**
Linolenic	9.29**	1.95	45.11**

* significant at 5% level
** significant at 1% level

Therefore, a scale could not be found which would be adequate (additive) for all three fatty acids in all three crosses.

Despite the inadequacies of the original scale, an analysis was carried out on the untransformed data.

Oleic Acid

(a) Self- and cross-pollinated seed on parental strains

The oleic acid content of SP (self-pollinated) seed from parental lines 1 and 2 differed significantly from each other (69.8% and 54.0% respectively) (Table 8). The oleic value of CP (cross-pollinated) seed harvested from parent 1 was 63.2% which differed significantly from the SP seed value of parent 1. The CP seed harvested from parent 2 had an oleic value of 56.8% which was greater but not significantly different from the SP seed value of parent 2. The reciprocally CP seed of 1 x 2 and 2 x 1 differed significantly for oleic acid content (63.2% and 56.8% respectively).

The oleic acid content of SP seed from parental lines 1 and 3 differed significantly from each other (69.8% and 42.6% respectively). The oleic value of CP seed harvested from parent 1 was 61.7% which differed significantly from the SP seed value of parent 1. The CP seed harvested from parent 3 had an oleic value of 52.8% which differed significantly from the SP seed value of parent 3. The reciprocally CP seed of 1 x 3 and 3 x 1 differed significantly for oleic acid content (61.7% and 52.8% respectively).

Table 8. Fatty acid composition of oil from self- and cross-pollinated seed from three strains of rape

Parent or cross	No. of plants	Fatty acids as percent of total fatty acids					
		Palmitic	Oleic	Linoleic	Linolenic	Eicosenoic	Erucic
1	10	4.6a*	69.8a	12.5a	12.3a	0.7a	t**
1 x 2	10	4.7a	63.2b	19.8b	11.5a	0.8a	t
2 x 1	10	5.2a	56.8c	23.8c	12.5a	1.9a	t
2	10	5.2a	54.0c	27.6c	11.5a	1.7a	t
1	10	4.6a	69.8a	12.5a	12.3a	0.7a	t
1 x 3	10	4.6a	61.7b	20.1b	12.6a	0.5a	t
3 x 1	10	5.3a	52.8c	26.5c	14.3b	1.4a	t
3	10	6.0a	42.6d	35.6d	15.4b	0.5a	t
2	10	5.1a	54.0a	27.2a	11.5a	1.4a	t
2 x 3	10	5.9a	47.5b	32.9b	12.8a	0.9a	t
3 x 2	8	5.8a	45.5b	33.8b	13.5a	1.5a	t
3	8	5.7a	42.6c	35.6b	15.5b	0.6a	t

* means of each fatty acid within each cross followed by the same letter are not significantly different at the 5% level (LSD)

** t = trace

The oleic acid content of SP seed from parental lines 2 and 3 differed significantly from each other (54.0% and 42.6% respectively). The oleic value of CP seed harvested from parent 2 was 47.5% which differed significantly from the SP seed value of parent 2. The CP seed harvested from parent 3 had an oleic value of 45.5% which was significantly different from the SP seed value of parent 3. The reciprocally CP seed of 2 x 3 and 3 x 2 did not differ significantly for oleic acid content (47.5% and 45.5% respectively).

These results indicate that oleic acid content is not completely controlled by the embryo genotype in crosses 1 x 2 and 1 x 3, but is significantly affected by the genotype of the maternal parent. The oleic value in cross 2 x 3 appears to be under embryo control.

(b) Self-pollinated seed on parental, F_1 and F_2 populations

The mean oleic acid content of F_1 and reciprocal F_1 (RF_1) populations did not differ significantly from each other in all three crosses (Table 9). The mean oleic acid content of F_2 and reciprocal F_2 (RF_2) populations did not differ significantly from each other in all three crosses (Table 10). These results indicated no cytoplasmic effects on oleic acid content.

The means and variances of F_1 and reciprocal F_1 (RF_1) populations did not differ significantly from each other. The F_2 and reciprocal F_2 (RF_2) populations did not differ significantly from each other. Therefore, the data of reciprocal populations were pooled for further analysis.

Table 9. Fatty acid composition of oil from self-pollinated seed from parental and F_1 populations

Parent or cross	No. of plants	Fatty acids as percent of total fatty acids					
		Palmitic	Oleic	Linoleic	Linolenic	Eicosenoic	Erucic
P_1	25	4.7a*	69.7a	12.8a	12.2a	0.7a	t**
F_1(1 x 2)	25	5.8b	61.5b	20.0b	12.4a	0.2a	t
RF_1(2 x 1)	25	5.7b	62.5b	19.6b	12.0a	0.2a	t
P_2	25	4.9a	54.2c	27.4c	12.0a	1.7b	t
P_1	25	4.7a	69.7a	12.8a	12.2a	0.7a	t
F_1(1 x 3)	25	5.5b	60.6b	20.8b	12.6a	0.5a	t
RF_1(3 x 1)	25	5.5b	60.9b	20.6b	12.3a	0.6a	t
P_3	25	6.0b	42.6c	35.6c	15.2b	0.5a	t
P_2	25	4.9a	54.2a	27.4a	12.0a	1.7a	t
F_1(2 x 3)	25	5.8b	51.8b	29.0b	12.2a	1.0b	t
RF_1(3 x 2)	25	6.0b	51.9b	29.2b	11.8a	1.0b	t
P_3	25	6.0b	42.6c	35.6c	15.2b	0.5b	t

* means of each fatty acid within each cross followed by the same letter are not significantly different at the 5% level (LSD)

** t = trace

Table 10. Fatty acid composition of oil from self-pollinated seed from F_2 and reciprocal F_2 (RF_2) populations

Population	Cross	No. of plants	Fatty acid as percent of total fatty acids					
			Palmitic	Oleic	Linoleic	Linolenic	Eicosenoic	Erucic
F_2	(1 x 2)	50	5.6a*	63.3a	18.8a	11.6a	0.9a	t**
RF_2	(2 x 1)	50	5.1a	64.1a	19.0a	10.8a	0.9a	t
F_2	(1 x 3)	50	5.3a	60.6a	21.3a	12.6a	0.3a	t
RF_2	(3 x 1)	50	5.3a	61.6a	20.0a	12.4a	0.9a	t
F_2	(2 x 3)	50	5.3a	54.0a	28.4a	11.7a	0.8a	t
RF_2	(3 x 2)	50	5.2a	53.6a	28.8a	11.8a	0.8a	t

* means of each fatty acid within each cross followed by the same letter are not significantly different at the 5% level (LSD)

** t = trace

The mean of the F_1 population of cross 1 x 2 (62.0%) was exactly the same as the mid-parent value (62.0%) indicating a simple additive gene system for oleic oil content (Table 11).

Table 11. Actual means and theoretical arithmetic means for oleic acid content

Population	Actual mean	Theoretical arithmetic mean	No. of plants
P_1	69.7		25
F_1 (1 x 2)	62.0	62.0	50
F_2 (1 x 2)	63.7	62.0	100
P_2	54.2		25
P_1	69.7		25
F_1 (1 x 3)	60.8	56.2	50
F_2 (1 x 3)	61.1	58.5	100
P_3	42.6		25
P_2	54.2		25
F_1 (2 x 3)	51.9	48.4	50
F_2 (2 x 3)	53.8	50.2	100
P_3	42.6		25

The F_2 population mean of cross 1 x 2 (63.7%) was only slightly higher than its expected arithmetic mean (62.0%) and also slightly higher than the mean of the F_1 population (62.0%). In cross 1 x 3 the F_1 population mean (60.8%) was higher than the mid-parent value (56.2%) indicating partial dominance of high oleic values. The F_2 population mean of cross 1 x 3 (61.1%) was higher than its expected arithmetic mean (58.5%) and

approximately equal to the F_1 population mean (60.8%).

In cross 2 x 3 the F_1 population mean (51.9%) was higher than the mid-parent value (48.4%), also indicating partial dominance of high oleic acid content. The F_2 plant population mean of cross 2 x 3 (53.8%) was higher than its expected arithmetic mean (50.2%) and also slightly higher than the F_1 population mean (51.9%).

The frequency distributions of the parents did not overlap in all three crosses (Table 12). The F_2 range in cross 1 x 2 was 50.9 - 73.7 percent, indicating no transgressive segregation. A high frequency of both parental types were recovered in the F_2 plant population, indicating that the oleic acid content is controlled by only a few gene pairs. The F_2 range in cross 1 x 3 was 45.8 - 71.6 percent, indicating no transgressive segregation. A high frequency of the P_1 parent type was recovered in the F_2 plant population. Only one F_2 plant fell within the range of the P_3 parent. This would support the conclusion of partial dominance indicated by F_1 means. The F_2 range of cross 2 x 3 was 45.1 - 60.7 percent, indicating no transgressive segregation. The great majority of F_2 plants fell in the P_2 parent range, further supporting the conclusion of partial dominance based on the F_1 means. Since transgressive segregation was not obtained in any of the segregating F_2 populations, it indicates that + and - gene factors were isodirectionally distributed in the parents.

The frequency distributions of oleic acid values of the single F_2 seed from F_1 plants (SF_2) were very similar to values of F_2 plants in crosses 1 x 2 and 1 x 3 (Table 12). In the cross of 2 x 3 the range of the values of single F_2 seeds was slightly greater than the self-pollinated F_2 plants.

Table 12. Frequency distribution based on oleic acid content

Population	Class centers in percent of oleic acid													Total No.	Mean	Variance
	38	41	44	47	50	53	56	59	62	65	68	71	74			
P_1										3	11	18	3	25	67.9	5.42
F_1 (1 x 2)							1	20	18	11				50	62.0	4.78
P_2					3	11	10	1						25	54.2	3.82
F_2 (1 x 2)					1	1	7	20	24	26	12	8	1	100	63.7	18.92
SF_2* (1 x 2)						11	14	20	23	25	5	3		100	61.4	19.42
P_1										3	11	18	3	25	69.7	5.42
F_1 (1 x 3)							5	21	18	6				50	60.8	5.53
P_3	2	12	9	2										25	42.6	4.44
F_2 (1 x 3)			1		1	11	19	14	22	18	10	4		100	61.1	22.47
SF_2 (1 x 3)						2	11	15	30	22	18	4		100	63.1	15.90
P_2					3	11	10	1						25	54.2	3.82
F_1 (2 x 3)				4	23	18	5							50	51.9	4.98
P_3	2	12	9	2										25	42.6	4.44
F_2 (2 x 3)			2	4	23	34	30	7						100	53.8	10.70
SF_2 (2 x 3)	5	5	5	24	20	16	14	10	1					100	50.6	19.68

* single F_2 seeds from F_1 plants

In the cross of 1 x 2 the mean of F_2 plants (63.7%) was slightly higher than the mean of single F_2 seed (61.4%) and the variance of F_2 plants (18.92) was slightly lower than the variance of single F_2 seed (19.42). In the cross of 1 x 3 the mean of F_2 plants (61.1%) was slightly lower than the mean of single F_2 seed (63.1%) and the variance of F_2 plants (22.47) was higher than the variance of single F_2 seed (15.94). In the cross of 2 x 3 the mean of F_2 plants (53.8%) was higher than the mean of single F_2 seed (50.6%) and the variance of F_2 plants (10.70) was lower than the variance of single F_2 seed (19.68).

Heritability estimates for oleic acid content were calculated according to the methods of Burton (1951), Mahmud and Kramer (1951) and Weber and Moorthy (1951). The heritability estimates based on F_2 plant values for cross 1 x 2 were 75%, 76% and 75% for the three methods respectively; for cross 1 x 3 were 75%, 78% and 77% respectively; and for cross 2 x 3 were 53%, 61% and 59% respectively (Table 13).

Table 13. Heritability (%) estimates for oleic acid content based on F_2 plant values

Formula	Cross		
	1 x 2	1 x 3	2 x 3
(1) $h^2 = \frac{VF_2 - VF_1}{VF_2}$	75	75	53
(2) $h^2 = \frac{VF_2 - (VP_1 \times VP_2)^{1/2}}{VF_2}$	76	78	61
(3) $h^2 = \frac{VF_2 - 1/3(VP_1 + VF_1 + VP_2)}{VF_2}$	75	77	59

Heritability estimates were calculated using the same formulas with the variance of the F_2 plant populations replaced by the variances of the single F_2 seed. The estimates were 75%, 77% and 76% respectively for cross 1 x 2; 65%, 69% and 68% respectively for cross 1 x 3; and 75%, 79% and 78% respectively for cross 2 x 3 (Table 14). The heritability

Table 14. Heritability (%) estimates for oleic acid content based on single F_2 seed values

Formula	Cross		
	1 x 2	1 x 3	2 x 3
(1)	75	65	75
(2)	77	69	79
(3)	76	68	78

estimates for the three different methods were in close agreement within each cross for oleic acid content. For crosses 1 x 2, 1 x 3 and 2 x 3, the average heritability estimates, based on F_2 plant values were 75%, 77% and 58% respectively. For crosses 1 x 2, 1 x 3 and 2 x 3, the average heritability estimates, based on single F_2 seed values were 76%, 67% and 77% respectively.

The application of Wrights' (1934), Weber's (1950) and Burton's (1951) procedures for calculating the minimum number of effective factors using F_2 plant values resulted in estimates of: 2.12, 2.11 and 2.12 respectively for cross 1 x 2; 5.42, 5.29 and 5.74 respectively for cross 1 x 3; and 2.94, 2.68 and 3.48 respectively for cross 2 x 3 (Table 15).

Table 15. Estimates of minimum number of effective factors conditioning oleic acid content based on F_2 plant values

Formula	Cross 1 x 2	Cross 1 x 3	Cross 2 x 3
(1) $k = \frac{(\bar{P}_1 - \bar{P}_2)^2}{8(VF_2 - VF_1)}$	2.12	5.42	2.94
(2) $k = \frac{(\bar{P}_1 - \bar{P}_2)^2}{8(VF_2 - 1/3(VP_1 + VF_1 + VP_2))}$	2.11	5.29	2.68
(3) $k = \frac{.25(.75 - h + h^2)(P_1 - P_2)^2}{VF_2 - VF_1}$	2.12	5.74	3.48

Estimates of minimum number of effective factors were calculated using the same formulas with the variances of the F_2 plant populations replaced by the variances of the single F_2 seed. The estimates were: 1.60, 1.59 and 1.62 respectively for cross 1 x 2; 8.82, 8.49 and 9.34 respectively for cross 1 x 3; and 1.15, 1.10 and 1.35 respectively for cross 2 x 3 (Table 16). The estimates for minimum number of effective factors by the three different methods were in close agreement within each cross. For crosses 1 x 2, 1 x 3, and 2 x 3, the minimum number of gene pairs, based on F_2 plant values were 2, 6 and 3 respectively. For crosses 1 x 2, 1 x 3 and 2 x 3, the minimum number of gene pairs, based on single F_2 seed values were 2, 9 and 1 respectively.

Table 16. Estimates of minimum number of effective factors conditioning oleic acid content based on single F_2 seed values

Formula	Cross		
	1 x 2	1 x 3	2 x 3
(1)	1.60	8.82	1.15
(2)	1.59	8.49	1.10
(3)	1.62	9.34	1.35

Linoleic Acid

(a) Self- and cross-pollinated seed on parental strains

The linoleic acid content of SP seed from parental lines 1 and 2 differed significantly from each other (12.5% and 27.6% respectively) (Table 17). The linoleic values of CP seed harvested from parent 1 was 19.8% which differed significantly from the SP seed value of parent 1. The CP seed harvested from parent 2 had a linoleic value of 23.8% which was less but not significantly different from the SP seed value of parent 2. The reciprocally CP seed of 1 x 2 and 2 x 1 differed significantly for linoleic acid content (19.8% and 23.8% respectively).

The linoleic acid content of SP seed from parental lines 1 and 3 differed significantly from each other (12.5% and 35.6% respectively). The linoleic value of CP seed harvested from parent 1 was

Table 17. Linoleic acid content of oil from self- and cross-pollinated seed from three strains of rapeseed

Linoleic acid as percent of total fatty acids					
Parent or cross		Parent or cross		Parent or cross	
1	12.5a*	1	12.5a	2	27.2a
1 x 2	19.8b	1 x 3	20.1b	2 x 3	32.9b
2 x 1	23.8c	3 x 1	26.5c	3 x 2	33.8b
2	27.6c	3	35.6d	3	35.6b

* means of each fatty acid for each group of parents and crosses followed by the same letter are not significantly different at the 5% level (LSD)

20.1% which differed significantly from the SP seed value of parent 1. The CP seed harvested from parent 3 had a linoleic value of 26.5% which differed significantly from the SP seed value of parent 3. The reciprocally CP seed of 1 x 3 and 3 x 1 differed significantly for linoleic acid content (20.1% and 26.5% respectively).

The linoleic acid content of the SP seed from parental lines 2 and 3 differed significantly from each other (27.2% and 35.6% respectively). The linoleic value of CP seed harvested from parent 2 was 32.9% which differed significantly from the SP seed value of parent 2. The CP seed harvested from parent 3 had a linoleic value of 33.8% which was not significantly different from the SP seed value of parent 3. The reciprocally CP seed of 2 x 3 and 3 x 2 did not differ significantly for linoleic content (32.9% and 33.8% respectively).

The results indicate that linoleic acid content is not completely controlled by the embryo genotype but is significantly affected by the genotype of the maternal parent in crosses 1 x 2 and 1 x 3. The linoleic value in cross 2 x 3 appears to be under embryo control.

(b) Self-pollinated seed on parental, F_1 and F_2 populations

The mean linoleic acid content of F_1 and reciprocal F_1 (RF_1) populations did not differ significantly from each other in all three crosses (Table 18). The mean linoleic acid content of F_2 and

Table 18. Linoleic acid content of oil from seed from F_1 and F_2 populations

Population	Linoleic acid as percent of total fatty acids		
	Cross 1 x 2	Cross 1 x 3	Cross 2 x 3
F_1	20.0	20.8	29.0
RF_1	19.6	20.6	29.2
F_2	18.8	21.3	28.4
RF_2	19.0	20.0	28.8

reciprocal F_2 (RF_2) populations did not differ significantly from each other in all three crosses (Table 18). These results indicated no cytoplasmic effects on linoleic acid content.

The means and variance of F_1 and reciprocal F_1 (RF_1)

populations were not significantly different; therefore data was pooled for further analysis. The F_2 and reciprocal F_2 (RF_2) populations were not significantly different; therefore data was pooled for further analysis.

The mean of the F_1 population of cross 1 x 2 (19.8%) was approximately equal to the mid-parent value (20.1%) indicating a simple additive gene system for linoleic acid content (Table 19).

Table 19. Actual means and theoretical arithmetic means for linoleic acid content

Population	Actual mean	Theoretical arithmetic mean	No. of plants
P_1	12.8		25
F_1 (1 x 2)	19.8	20.1	50
F_2 (1 x 2)	18.9	20.0	100
P_2	27.4		25
P_1	12.8		25
F_1 (1 x 3)	20.8	24.2	50
F_2 (1 x 3)	20.6	22.5	100
P_3	35.6		25
P_2	27.4		25
F_1 (2 x 3)	29.1	31.5	50
F_2 (2 x 3)	28.6	30.2	100
P_3	35.6		25

The F_2 population mean of cross 1 x 2 (18.9%) was less than its expected arithmetic mean (20.0%) and also slightly less than the mean of the F_1 population (19.8%).

In cross 1 x 3 the F_1 population mean (20.8%) was lower than the mid-parent value (24.2%) indicating partial dominance of low linoleic values. The F_2 population mean of cross 1 x 3 (20.6%) was lower than its expected arithmetic mean (22.5%) but approximately equal to the F_1 population mean (20.6%).

In cross 2 x 3 the F_1 population mean (29.1%) was less than the mid-parent value (31.5%), also indicating partial dominance of low linoleic acid values. The F_2 plant population mean of cross 2 x 3 (28.6%) was less than its expected arithmetic mean (30.2%) and also slightly less than the F_1 population mean (29.1%).

The frequency distribution of the parent did not overlap in all three crosses (Table 20). The F_2 range in cross 1 x 2 was 12.1 - 26.8 percent, indicating no transgressive segregation. A high frequency of both parental types were recovered in the F_2 plant population. This would indicate that the linoleic acid content is controlled by a few gene pairs. The F_2 range in cross 1 x 3 was 13.2 - 29.7 percent, indicating no transgressive segregation. A high frequency of the P_1 parent type was recovered in the F_2 population and no F_2 plants fell within the range of the P_3 parent. This would support the conclusion of partial dominance indicated by the F_1 mean. The F_2 range of cross 2 x 3 was 23.8 - 34.3 percent, indicating no transgressive segregation. The great majority of F_2 plants fell in the P_2 range, supporting the conclusion of partial dominance based on

Table 20. Frequency distributions based on linoleic acid content

Population	Class centers in percent of linoleic acid																Total No.	Mean	Variance
	10	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40			
P_1	2	13	7	3													25	12.8	2.82
F_1 (1 x 2)				2	9	29	10										50	19.8	2.09
P_2								1	11	9	4						25	27.4	2.69
F_2 (1 x 2)		5	14	13	17	18	21	9	3								100	18.9	12.80
SF_2* (1 x 2)		1	3	10	14	24	15	16	12	5							100	21.1	14.66
P_1	2	13	7	3													25	12.8	2.82
F_1 (1 x 3)					8	20	17	3	2								50	20.8	2.99
P_3												2	11	7	3	2	25	35.6	3.82
F_2 (1 x 3)			14	11	17	12	14	16	7	6	2						100	20.6	16.98
SF_2 (1 x 3)		1	9	11	27	26	13	5	7	1							100	19.7	10.54
P_2								1	11	9	4						25	27.4	2.69
F_1 (2 x 3)								1	7	15	21	6					50	29.1	2.80
P_3												2	11	7	3	2	25	35.6	3.82
F_2 (2 x 3)								5	21	33	25	11	5				100	28.6	5.36
SF_2 (2 x 3)								11	12	23	27	17	7	4			100	29.3	7.65

* single F_2 seeds from F_1 plants

the F_1 means. Since transgressive segregation was not obtained in the segregating F_2 populations it indicates that + and - factors were isodirectionally distributed in the parents. Since the range of the F_2 distributions in crosses 1 x 2 and 2 x 3 included the values of both parental types, the number of effective factors or genes conditioning linoleic acid content is not likely to be large.

The frequency distributions of linoleic acid values of the single F_2 seed from F_1 plants (SF_2) were similar to the range of F_2 plants (Table 20).

In the cross of 1 x 2 the mean of F_2 plants (18.9%) was lower than the mean of single F_2 seed (21.1%) and the variance of F_2 plants (12.80) was also lower than the variance of single F_2 seed (14.66). In the cross of 1 x 3 the mean of F_2 plants (20.6%) was slightly higher than the mean of single F_2 seed (19.7%) and the variance of F_2 plants (16.89) was higher than the variance of single F_2 seed (10.54). In the cross of 2 x 3 the mean of F_2 plants (28.6%) was slightly lower than the mean of single F_2 seed (29.3%) and the variance of F_2 plants (5.36) was lower than the variance of single F_2 seed (7.66).

Heritability estimates for linoleic acid content were calculated according to the methods of Burton (1951), Mahmud and Kramer (1951) and Weber and Moorthy (1951). Heritability estimates based on F_2 plant values for cross 1 x 2 were 84%, 79% and 80% for the three methods respectively; for cross 1 x 3 were 82%, 81% and 81% respectively; and for cross 2 x 3 were 48%, 40% and 42% respectively (Table 21).

Heritability estimates were calculated using the same formulas with the variances of the F_2 plant populations replaced by

Table 21. Heritability (%) estimates for linoleic acid content based on F_2 plant values

Formula	Cross		
	1 x 2	1 x 3	2 x 3
(1)	84	82	48
(2)	79	81	40
(3)	80	81	42

the variances of the single F_2 seed. The estimates were 86%, 81% and 83% respectively for cross 1 x 2; 72%, 69% and 70% respectively for cross 1 x 3; and 63%, 58% and 60% respectively for cross 2 x 3 (Table 22).

Table 22. Heritability (%) estimates for linoleic acid content based on single F_2 seed values

Formula	Cross		
	1 x 2	1 x 3	2 x 3
(1)	86	72	63
(2)	81	69	58
(3)	83	70	60

The heritability estimates for the three methods were in close agreement within each cross for linoleic acid content. For crosses 1 x 2, 1 x 3 and 2 x 3, the heritability estimates, based on F_2 plant values averaged 81%, 81% and 43% respectively. For crosses 1 x 2, 1 x 3 and

2 x 3, the heritability estimates based on single F_2 seed, averaged 83%, 70% and 60% respectively.

The application of Wrights' (1934), Weber's (1951) and Burton's (1951) procedures for calculating the minimum number of effective factors based on F_2 plant values resulted in estimates of: 2.49, 2.60 and 2.49 respectively for cross 1 x 2; 4.65, 4.72 and 4.85 respectively for cross 1 x 3; and 3.28, 3.71 and 3.84 respectively for cross 2 x 3 (Table 23). Estimates of minimum number of effective

Table 23. Estimates of minimum number of effective factors conditioning linoleic acid content based on F_2 plant values

Formula	Cross		
	1 x 2	1 x 3	2 x 3
(1)	2.49	4.65	3.28
(2)	2.60	4.72	3.71
(3)	2.49	4.85	3.84

factors were calculated using the same formulas with the variance of the F_2 plant populations replaced by the variances of the single F_2 seed. The estimates were: 2.12, 2.20 and 2.12 respectively for cross 1 x 2; 8.61, 8.87 and 8.99 respectively for cross 1 x 3; and 1.73, 1.85 and 2.03 respectively for cross 2 x 3 (Table 24). The estimates for number of effective factors by the three different methods were in close agreement. For crosses 1 x 2, 1 x 3 and 2 x 3, the minimum number of gene pairs based on F_2 plant values were 3, 5 and 4 respectively.

Table 24. Estimates of minimum number of effective factors conditioning linoleic acid content based on single F_2 seed values

Formula	Cross		
	1 x 2	1 x 3	2 x 3
(1)	2.12	8.61	1.73
(2)	2.20	8.87	1.85
(3)	2.12	8.99	2.03

For crosses 1 x 2, 1 x 3 and 2 x 3, the minimum number of gene pairs based on single F_2 seed values were 2, 9 and 2 respectively.

Linolenic Acid

(a) Self- and cross-pollinated seed on parental strains

The linolenic acid content of SP seed from parental lines 1 and 2 did not differ significantly from each other (12.3% and 11.5% respectively) (Table 25). No inferences could be drawn from the cross 1 x 2.

The linolenic acid content of SP seed from parental lines 1 and 3 differed significantly from each other (12.3% and 15.4% respectively). The linolenic value of CP seed harvested from parent 1 was 12.6% which did not differ significantly from the SP seed value of parent 1. The CP seed harvested from parent 3 had a linolenic value of 14.3% which was less than but not significantly different from the SP seed value of parent 3. The reciprocally CP seed of 1 x 3 and 3 x 1 differed

Table 25. Linolenic acid content of oil from self- and cross-pollinated seed from three strains of rapeseed

Linolenic acid as percent of total fatty acids					
Parent or cross		Parent or cross		Parent or cross	
1	12.3a*	1	12.3a	2	11.5a
1 x 2	11.5a	1 x 3	12.6a	2 x 3	12.8a
2 x 1	12.5a	3 x 1	14.3b	3 x 2	13.5a
2	11.5a	3	15.4b	3	15.5b

* means of each fatty acid for each group of parents and crosses followed by the same letter are not significantly different at the 5% level (LSD)

significantly for linolenic acid content (12.6% and 14.3% respectively).

The linolenic acid content of SP seed from parental lines 2 and 3 differed significantly from each other (12.3% and 15.5% respectively). The linolenic acid value of CP seed harvested from parent 1 was 12.8% which was higher but not significantly different from the SP seed value of parent 2. The CP seed harvested from parent 3 had a linolenic value of 13.5% which was significantly different from the SP seed value of parent 3. The reciprocally CP seed of 2 x 3 and 3 x 2 did not differ significantly for linolenic acid content (12.8% and 13.5% respectively).

These results indicate that linolenic acid content is controlled largely by the genotype of the maternal parent rather than the embryo genotype in cross 1 x 3. The linolenic content in cross 2 x 3 appeared to be under embryo control.

(b) Self-pollinated seed on parental, F_1 and F_2 populations

The mean linolenic acid content of F_1 and reciprocal F_1 (RF_1) populations did not differ significantly from each other in all three crosses (Table 26). The mean linolenic acid content of F_2 and reciprocal

Table 26. Linolenic acid content of oil from seed from F_1 and F_2 populations

Population	Linolenic acid as percent of total fatty acids		
	Cross 1 x 2	Cross 1 x 3	Cross 2 x 3
F_1	12.4	12.6	12.2
RF_1	12.0	12.3	11.8
F_2	11.6	12.6	11.7
RF_2	10.8	12.4	11.8

F_2 (RF_2) populations did not differ significantly from each other in all three crosses (Table 26). These results indicated no cytoplasmic effect on linolenic acid content.

The means and variances of F_1 and reciprocal F_1 (RF_1) populations did not differ significantly from each other. The means and variances of F_2 and reciprocal F_2 (RF_2) populations did not differ significantly from each other. Therefore data for reciprocal populations were pooled for further analysis.

The mean of the F_1 population of cross 1 x 3 (12.4%) was essentially the same as the low linolenic parent P_1 (12.2%) indicating

dominance of low linolenic acid content (Table 27). The F_2 population mean of cross 1 x 3 (12.5%) was lower than its expected arithmetic mean (13.2%) but was approximately equal to the F_1 population mean (12.4%).

Table 27. Actual means and theoretical arithmetic means for linolenic acid content

Population	Actual mean	Theoretical arithmetic mean	No. of plants
P_1	12.2		25
F_1 (1 x 2)	12.2	12.1	50
F_2 (1 x 2)	11.2	12.1	100
P_2	12.0		25
P_1	12.2		25
F_1 (1 x 3)	12.4	13.7	50
F_2 (1 x 3)	12.5	13.2	100
P_3	15.2		25
P_2	12.0		25
F_1 (2 x 3)	12.2	13.6	50
F_2 (2 x 3)	11.7	13.1	100
P_3	15.2		25

In cross 2 x 3 the F_1 population mean (12.2%) was essentially the same as the low linolenic parent P_2 (12.0%), also indicating dominance of low linolenic acid content. The F_2 population mean of cross 2 x 3 (11.7%) was less than its expected arithmetic mean (13.1%) and also lower than the mean of the low linolenic parent P_2 (12.0%).

The frequency distributions of linolenic acid values for the

three parents, although narrow, overlapped each other in all three crosses (Table 28). However, the overlap in crosses 1 x 3 and 2 x 3 was only slight.

The F_2 range in cross 1 x 2 was 7.8 - 17.5 percent, indicating transgressive segregation for both high and low linolenic acid values. The F_2 range in cross 1 x 3 was 8.4 - 15.7 percent, indicating transgressive segregation in the direction of low linolenic acid. The great majority of F_2 plants fell in the P_1 range, further supporting the conclusion of dominance based on the F_1 mean. The F_2 range in cross 2 x 3 was 9.0 - 15.6 percent, also indicating transgressive segregation in the direction of low linolenic acid. The great majority of F_2 plants fell in the P_2 range, further supporting the conclusion of dominance based on the F_1 mean. Since transgressive segregation was obtained in the segregating populations, it is indicated that + and - factors were non-isodirectionally distributed in the parents.

The frequency distributions of linolenic acid values of the single F_2 seed from F_1 plants (SF_2) were very similar to the bulk analysis of F_2 plants in crosses 1 x 2 and 1 x 3. In the cross of 2 x 3 the range of values of single F_2 seed was much greater than the self-pollinated F_2 plants and indicated transgressive segregation in both directions.

In the cross of 1 x 2 the mean of F_2 plants (11.2%) was essentially the same as the mean of single F_2 seed (11.3%) and the variance of F_2 plants (2.14) was slightly higher than the variance of single F_2 seed (1.82). In the cross of 1 x 3 the mean of F_2 plants (12.5%) was slightly higher than the mean of single F_2 seed (11.9%) and the variance of F_2 plants (1.78) was also slightly higher than the

Table 28. Frequency distribution based on linolenic acid content

Population	Class centers in percent of linolenic acid																Total No.	Mean	Variance
	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22			
P_1				1	6	9	8	1									25	12.2	0.81
F_1 (1 x 2)				3	9	22	11	4	1								50	12.2	1.12
P_2				2	9	8	5	1									25	12.0	0.94
F_2 (1 x 2)		4	8	21	28	24	11	3			1						100	11.2	2.14
SF_2* (1 x 2)	1		8	16	39	21	8	5	1	1							100	11.3	1.82
P_1				1	6	9	8	1									25	12.2	0.81
F_1 (1 x 3)				3	8	18	12	8	1								50	12.4	1.14
P_3						1		8	10	4	1	1					25	15.2	1.16
F_2 (1 x 3)		1	1	5	18	30	22	16	6	1							100	12.5	1.78
SF_2 (1 x 3)		1	3	8	26	32	21	6	3								100	11.9	1.52
P_2				2	9	8	5	1									25	12.0	0.94
F_1 (2 x 3)				2	12	18	13	5									50	12.2	0.91
P_3						1		8	10	4	1	1					25	15.2	1.16
F_2 (2 x 3)			2	13	32	32	13	5	2	1							100	11.7	1.40
SF_2 (2 x 3)	1	1	2	12	20	19	8	10	13	4	2	4	2		1	1	100	12.9	4.23

* single F_2 seeds from F_1 plants

variance of single F_2 seed (1.52). In the cross of 2 x 3 the mean of F_2 plants (11.7%) was less than the mean of single F_2 seed (12.9%) and the variance of F_2 plants (1.40) was much lower than the variance of single F_2 seed (4.23).

Heritability estimates for linolenic acid content were calculated according to the methods of Burton (1951), Mahmud and Kramer (1951) and Weber and Moorthy (1951). Based on F_2 plants the estimates were: 48%, 59% and 55% respectively for cross 1 x 2; 36%, 46% and 42% respectively for cross 1 x 3; and 35%, 26% and 29% respectively for cross 2 x 3 (Table 29). Heritability estimates calculated using the

Table 29. Heritability (%) estimates for linolenic acid content based on F_2 plant values

Formula	Cross		
	1 x 2	1 x 3	2 x 3
(1)	48	36	35
(2)	59	46	26
(3)	55	42	29

same formulas based on single F_2 seed values were: 39%, 47% and 52% respectively for cross 1 x 2; 25%, 32% and 36% respectively for cross 1 x 3; and 79% 76% and 75% respectively for cross 2 x 3 (Table 30). The heritability estimates for the three methods did not agree as closely within each cross for linolenic acid as they did for oleic and linoleic acid. For crosses 1 x 2, 1 x 3 and 2 x 3, the heritability

Table 30. Heritability (%) estimates for linolenic acid content based on single F_2 seed values

Formula	Cross		
	1 x 2	1 x 3	2 x 3
(1)	39	25	79
(2)	47	32	76
(3)	52	36	75

estimates, based on F_2 plant values, averaged 54%, 41% and 30% respectively. For crosses 1 x 2, 1 x 3 and 2 x 3, the heritability estimates, based on single F_2 seed values, averaged 46%, 31% and 77% respectively.

The application of Wrights' (1934), Weber's (1951) and Burton's (1951) procedures for calculating the minimum number of effective factors based on F_2 plant values resulted in values of: 0.005, 0.004 and 0.007 respectively for cross 1 x 2; 1.75, 1.51 and 2.40 respectively for cross 1 x 3; and 2.57, 3.17 and 3.56 respectively for cross 2 x 3 (Table 31).

Table 31. Estimates of minimum number of effective factors conditioning linolenic acid content based on F_2 plant values

Formula	Cross		
	1 x 2	1 x 3	2 x 3
(1)	0.005	1.75	2.57
(2)	0.004	1.51	3.17
(3)	0.007	2.40	3.56

Estimates of minimum number of effective factors were calculated using the same formula based on single F_2 seed values. The estimates were: 0.007, 0.006 and 0.011 respectively for cross 1 x 2; 2.93, 2.33 and 4.03 respectively for cross 1 x 3; and 0.39, 0.40 and 0.53 respectively for cross 2 x 3 (Table 32).

Table 32. Estimates of minimum number of effective factors conditioning linolenic acid content based on single F_2 seed values

Formula	Cross		
	1 x 2	1 x 3	2 x 3
(1)	0.007	2.93	0.39
(2)	0.006	2.33	0.40
(3)	0.011	4.03	0.53

The estimates for the minimum number of effective factors by the three different methods were in reasonable agreement. For the cross 1 x 2, no genetic differences were indicated, as could be expected from the parental phenotypic values. For the crosses 1 x 3 and 2 x 3 the minimum number of gene pairs based on F_2 plant values were 2 and 3 respectively. For the crosses 1 x 3 and 2 x 3 the minimum number of gene pairs based on single F_2 seed values were 3 and 1 respectively.

Correlation Coefficients

A significant high negative correlation between oleic and linoleic was observed in all populations (-.96 to -.68) except in P_3

(-.35) (Table 33). In crosses 1 x 2, 1 x 3 and 2 x 3 the correlations in the F_2 were -.92, -.96 and -.92 respectively. A significant negative correlation was also observed between oleic and linolenic in all populations. However, the coefficients were generally of a lower magnitude than for oleic and linoleic (-.75 to -.58). In crosses 1 x 2, 1 x 3 and 2 x 3 the correlations in the F_2 were -.63, -.58 and -.71 respectively. The correlations between linoleic and linolenic varied from a significant positive correlation of .55 in the F_1 (1 x 3), to a negative correlation of -.31 in the P_3 population. However, in the segregating populations all correlations were positive and significant. In crosses 1 x 2, 1 x 3 and 2 x 3 the correlations in the F_2 were .43, .40 and .52 respectively.

Table 33. Simple correlation coefficients for pairs of fatty acids for parental, F_1 and F_2 populations

Population	Oleic and Linoleic	Oleic and Linolenic	Linoleic and Linolenic
P_1	-.77**	-.60**	.30
F_1 (1 x 2)	-.68**	-.66**	.45**
F_2 (1 x 2)	-.92**	-.63**	.43**
P_2	-.83**	-.57**	.40*
P_1	-.77**	-.60**	.30
F_1 (1 x 3)	-.83**	-.75**	.55**
F_2 (1 x 3)	-.96**	-.58**	.40**
P_3	-.35	-.61**	-.31
P_2	-.83**	-.57**	.40*
F_1 (2 x 3)	-.72**	-.58**	.43**
F_2 (2 x 3)	-.92**	-.71**	.52**
P_3	-.35	-.61**	-.31

** significant at 1% level

* significant at 5% level

DISCUSSION

This study has attempted to separate maternal effect on fatty acid composition of the seed into two categories: the effect of maternal nuclear genotype on the fatty acid composition of the seed; and the cytoplasmic effect on fatty acid values of the F_1 and F_2 populations.

When comparing the fatty acid composition of SP and CP seed on the same maternal parent, the sporophyte genotype and cytoplasm of the embryo cells is assumed to be the same. Only the embryo nuclear genotypes are different. If SP and CP values are identical on each maternal plant, then the fatty acid composition of the seed is completely controlled by the maternal parent genotype. This has been demonstrated in soybeans (Brim et al. 1968). The comparison of reciprocally CP seed on the two different parental lines assumes that only the embryo nuclear genotype is the same. If the reciprocally CP seed is the same, then there is complete embryo control. This has been found for eicosenoic and erucic acid in rapeseed (Downey and Harvey 1963) and oleic and linoleic acid in safflower (Knowles and Hill 1964). This study indicates that there is a definite maternal genotype effect on the oleic, linoleic and linolenic acid content of the seed in crosses 1 x 2 and 1 x 3 but maternal control is not complete. The 2 x 3 cross indicates largely embryo control with only a small maternal genotype effect. These variable results are similar to those in corn (Jellum 1966), flax (Yermanos and Knowles 1962), and soybean (Brim et al. 1968).

The comparison of two reciprocal F_1 populations assumes that the cytoplasm of the embryo cells and the sporophyte cells is the same within each population but is different from its reciprocal. However, the nuclear genotype of the sporophyte of both F_1 populations and the constitution of embryo nuclear genotypes are the same. Reciprocal F_1 and F_2 populations showed no significant differences in means or variances. This study clearly indicates that no significant cytoplasmic effects were evident for oleic, linoleic and linolenic acids. This is unlike the variable results presented for corn where F_1 reciprocal differences were in evidence for oleic and linoleic acid content in some combinations but not in others (Poneleit and Bauman 1970; de la Roche et al. 1971).

The seed analyzed in this study was produced under field conditions. A larger difference in fatty acid composition between parental lines was obtained than in a preliminary study performed in the greenhouse (Kondra and Stefansson 1970). There was less variability in fatty acid composition within lines in the field grown material than in the greenhouse produced material.

The relative content of C-18 fatty acids is strongly influenced by environmental conditions (Craig 1961). It is possible that maternal effects on C-18 fatty acid composition could be due to genotypic differences in the time of flowering, period from flowering to seed maturity, and time of seed maturity. The strains used in this study, however, were selected for similar flowering and maturity time. In this study, the three strains flowered and matured at essentially the same time and therefore differences in rate and time of maturation should not be a significant factor.

Partial dominance for high oleic and low linoleic content was indicated in crosses 1 x 3 and 2 x 3. In cross 1 x 2, however, a simple additive gene system is indicated for oleic and linoleic values. The results for oleic acid are similar to those in flax (Comstock et al. 1960) in which partial dominance was indicated for high oleic acid. The results for linoleic are unlike those presented in corn where a single dominant gene was indicated (de la Roche et al. 1971; Poneleit 1972) and safflower where partial dominance for high linoleic values was indicated (Yermanos et al. 1967). Dominance of low linolenic values was indicated in this study. This is similar to the results in soybean (White et al. 1961) and unlike the results in flax where partial dominance for low linolenic values was indicated (Comstock et al. 1960).

The three methods used to calculate broad sense heritability estimates differed only in the number of populations used in estimating environmental variances. Environmental variance was derived from F_1 variance in Burton's method, from the square root of the product of the parental variances in Mahmud and Kramer's method, and from the pooled variances of the three non-segregating populations in Weber and Moorthy's method. The last method should give the best heritability estimates as all three non-segregating populations were utilized in estimating environmental variance. The calculated heritability estimates based on the three methods were similar within each cross for all three fatty acids since the variances of the non-segregating populations were similar. The average broad sense heritability estimates for oleic acid content in crosses 1 x 2, 1 x 3 and 2 x 3, based on F_2 plant values, were 75%, 77% and 58% respectively. These results for oleic acid are similar to those in flax where a high heritability was indicated for

oleic acid content (Comstock et al. 1960).

The average broad sense heritability estimates for linoleic acid content in crosses 1 x 2, 1 x 3 and 2 x 3, based on F_2 plant values, were 81%, 81% and 43% respectively. These results for linoleic acid were unlike those in flax where the percent linoleic acid had a very low heritability (Comstock et al. 1960).

The average broad sense heritability estimates for linolenic acid content in crosses 1 x 2, 1 x 3 and 2 x 3, based on F_2 plant values, were 54%, 41% and 30% respectively. This is unlike the results presented for flax where linolenic acid was highly heritable (Comstock et al. 1960).

The first two methods used to calculate minimum number of effective factors differed only in the number of populations used in estimating environmental variances. Environmental variance was derived from F_1 variance in Castle and Wright's method and from the pooled variances of the three non-segregating populations in Weber's method. The third method (Burton's) takes into account the minimal effect of dominance on the estimate of minimum number of effective factors. The second method should give the best estimate of minimum number of effective factors, where no dominance exists, as all three non-segregating populations were utilized in estimating environmental variance. Where dominance exists, as in crosses 1 x 3 and 2 x 3 for all fatty acids, the third method should provide the best estimate. However, the calculated estimates of minimum number of effective factors based on the three methods were similar within each cross. The average estimates of minimum number of effective factors based on F_2 plant values in crosses 1 x 2, 1 x 3 and 2 x 3 indicated the number of gene pairs controlling oleic acid are 2, 6 and 3 respectively. The average estimates of number

of effective factors based on F_2 plant values in crosses 1 x 2, 1 x 3 and 2 x 3 indicated the minimum number of gene pairs controlling linoleic acid are 3, 5 and 4 respectively. These variable estimates of number of effective factors are unlike the results in safflower where a single locus controlled relative oleic and linoleic acid content (Yermanos et al. 1967) and in corn where two loci controlled the levels of oleic and linoleic acid content (de la Roche et al. 1971).

The average estimates of minimum number of effective factors based on F_2 plant values indicated no genetic differences in cross 1 x 2 for linolenic acid content. However, there was segregation in the F_2 population. This could be due to non-isodirectional distribution of + and - factors in the parental lines. For crosses 1 x 3 and 2 x 3 the average estimate of minimum number of factors controlling linolenic acid were 2 and 3 respectively.

Correlation coefficients indicated that oleic is negatively correlated with linoleic and with linolenic, while linoleic and linolenic is positively correlated. In the F_2 segregating generations the correlations between oleic and linoleic, oleic and linolenic and linoleic and linolenic averaged -.93, -.64 and .45 respectively. The correlation between oleic and linoleic, oleic and linolenic and linoleic and linolenic are of the same magnitude and sign as those reported by Stefansson and Storgaard (1969). These results are also similar to those reported for summer turnip rape (Gross and Stefansson 1966), safflower (Yermanos et al. 1967), corn (Poneleit and Bauman 1970), flax (Comstock et al. 1960), and soybean (Howell and Collins 1957; White et al. 1961).

The genetic behavior of oleic and linoleic acid content within each cross was very similar. In cross 1 x 2, simple additive gene

action was observed for both oleic and linoleic. Partial dominance of oleic and linoleic values was observed in both crosses 1 x 3 and 2 x 3. Very similar heritabilities, number of effective factors based on F_2 plant values, and an extremely high negative correlation between the two fatty acids was observed within each cross. Therefore, the relative ratios of oleic and linoleic acid content are probably under the control of one genetic system. However, the number of gene pairs involved and gene action is not the same in all crosses.

One of the objectives in rapeseed breeding programs is to increase the linoleic acid content and decrease the linolenic acid content of the oil. In the populations under study, no transgressive segregation was indicated for oleic and linoleic acid. An extremely high negative correlation between oleic and linoleic was observed indicating the possibility of decreasing oleic and increasing linoleic acid content. Transgressive segregation was indicated for low linolenic acid. However, no very low linolenic acid content plants were identified. The positive correlations between linoleic and linolenic in segregating populations ranged from .43 to .53. These are not of such a large magnitude to preclude the development of high linoleic, low linolenic genotypes.

Several possible methods could be used to increase linoleic and decrease linolenic acid content. Introducing new genetic variability by induced mutations is one possible method for increasing linoleic and decreasing linolenic acid content. However, Brassica napus is an amphidiploid and masking of desirable mutants could occur due to the buffering effect of the two genomes. The introduction of new genetic

variability for linoleic and linolenic acid from cultivated or wild selections of Brassica species would be difficult. The inheritance of oleic, linoleic and linolenic acid content can be complicated by erucic content. Most wild Brassica species contain significant amounts of erucic acid which is under embryo control. Low erucic acid types would have to be isolated before oleic, linoleic and linolenic acid content could be evaluated. The low heritability of linolenic acid would indicate difficulty in selection for low linolenic acid and subsequent transfer to adapted cultivars.

The linoleic acid content of P_3 (35%) is considerably higher than existing Brassica napus cultivars (20%). The heritabilities and number of effective factors estimated in the two crosses involving P_3 would indicate that it should not be difficult to transfer the high linoleic character to low erucic, low glucosinolate cultivars through a straight back-cross or by a pedigree method or a combination of both.

This study has indicated that it would be difficult to predict the results of crosses of the material in this study with other material as there are differing degrees of maternal and embryo control. Each cross with new material may have different genetic behavior, especially in crosses of material containing erucic acid which is under embryo control. This study clearly indicates that cytoplasmic effects would likely be of no concern to a plant breeding program.

Broad sense heritabilities based on single F_2 seed values in cross 1 x 2 were similar to the estimates based on F_2 plant values for oleic (76% and 75% respectively) and linoleic (83% and 81% respectively) and were lower for linolenic acid (46% and 54% respectively). In cross

1 x 3 the heritability estimates based on single F_2 seed values were lower than estimates based on F_2 plant values for oleic (67% and 77% respectively), linoleic (70% and 81% respectively) and linolenic acid (31% and 41% respectively). In cross 2 x 3 the heritability estimates based on single F_2 seed values were much higher than estimates based on F_2 plant values for oleic (77% and 58% respectively), linoleic (60% and 43% respectively) and linolenic acid (77% and 30% respectively).

Estimates of minimum number of effective factors based on single F_2 seed values in cross 1 x 2 were similar to estimates based on F_2 plant values for oleic (2 and 2 respectively), linoleic (2 and 3 respectively) and linolenic (0 and 0 respectively) acid. In cross 1 x 3 the estimates of minimum number of effective factors based on single F_2 seed values were higher than estimates based on F_2 plant values for oleic (9 and 6 respectively), linoleic (9 and 5 respectively) and linolenic (3 and 2 respectively) acid. In cross 2 x 3 the estimates of minimum number of effective factors based on single F_2 seed values were lower than the estimates based on F_2 plant values for oleic (1 and 3 respectively), linoleic (2 and 4 respectively) and linolenic (1 and 3 respectively) acid.

Where both maternal and embryo control was observed the single F_2 seed estimates of heritability for all three fatty acids remained the same in cross 1 x 2 and decreased in cross 1 x 3. Estimates of number of effective factors for all three fatty acids were similar in cross 1 x 2 and increased in cross 1 x 3. However, where primarily embryo control was observed (2 x 3) the estimates of heritability based on single F_2 seed were higher and the number of

effective factors lower for all three fatty acids. Because of the variable effect of maternal and embryo genotype on the fatty acid composition, there is no distinct advantage of the "half-seed" technique (Downey and Harvey 1963) over conventional methods.

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